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THE VEGETATION OF CRANBERRY ISLAND (OHIO) AND ITS RELATIONS TO THE SUBSTRATUM, TEMPERATURE, AND EVAPORATION.[1] I

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(WITH SEVEN FIGURES)

The object of the present paper is to give, as briefly as is consistent with a limited presentation, the major conditions of some of the factors which have been found limiting the activity of plants in bogs.

The striking discontinuity of bogs in distribution, the absence of genetic relationship between bog plants and the surrounding flora of states in the latitude of Ohio, and the floristic agreement of these plants with the vegetation of the distant north has invited the attention of many students of ecology.

As early as 1872 a solution of this interesting problem had been formulated by GRAY (**14**) in his glacial relict theory. A similar explanation has been advanced by numerous recent writers, and the broader relations which involve comparative studies have been well established (**31**). However, the reciprocal relations of these plants and their habitat, the demands which the plants make on their environment, the means which they employ, and the functional rôle which the particular species perform; in short, an investigation of factors by which the present associations are determined and which would account for the existence and the peculiarities, structural and functional, of these "boreal" plants

[1] Contribution from the Botanical Laboratory, Ohio State University, no. 61.

on the basis of their relation to the present ecological conditions of their habitat, this has been a far more difficult matter and has not met with unanimity of opinion. A knowledge of the flora of a region and the floristic status of successive periods of time is indispensable, if for no other reason than to indicate the various conditions frequented by species or groups of plants. But the statistical method must be supplemented by an adequate study of experimental tests. The varying activity of plants as individuals and communities is of greatest importance scientifically and must be determined in the field under measured conditions.

Various theories have been put forward from time to time as to the environmental relations of plants in bogs, but none of them can be said to have brought nearer a solution of this phase of the problem. The historical aspect of the question need not be dealt with here in detail. The more important theories are those advanced by the following writers: KIHLMAN (19) regards low temperature and strong drying winds as the prominent factors in high northern latitudes; SCHIMPER (29) emphasizes humus acids in the soil, abundance of soluble salts and alkalies, and regards bog habitats as being "physiologically dry"; LIVINGSTON (22) suggests the presence of chemical substances not in direct relation to acidity of the soil as acting on the vegetation; WARMING (32) is inclined to look upon the presence of free humus acids as the weightiest cause; FRÜH and SCHRÖTER (13) correlate the conditions with low temperature and lack of aeration in the soil; while SCHWENDENER (30) and CLEMENTS (5) hold that the structural peculiarities are not at all related to present habitat conditions but are primitive peculiarities, which now remain unaltered but were originally developed under different xerophytic conditions. Another explanation, that of the toxicity of the habitat, and its consequent physiological aridity and selective operation upon forms striving for occupancy, has been offered by the writer of this paper. This view has come from a more detailed investigation of the physical and chemical characteristics of bog soils and their physiological property (7, 8). It emphasizes the active participation of specific microorganisms and fungi, a view which correlates also very well with the unproductiveness of differ-

ent peat soils under cultivation examined by the writer, and lays stress not alone upon structural characteristics in plants but also upon limiting habitat conditions as conducive to the development of place-functions. That various factors enter into the problem, and possibly many others not yet discovered have a part directly or indirectly, is clearly recognized.

Further field work on the bog plant societies has been carried out especially with a view to test the reference made by several writers to the part played by low substratum temperature and by the evaporating power of the air. In addition, studies on the physical, chemical, and biological problems of the substratum were continued.

It is obvious that the physical conditions, whether temperature or evaporation, if sufficiently great in their differences, must have an important bearing on the question of distribution and of xerophytism in bog plants. The larger part of the body of bog plants is imbedded in the peat at various depths. The various functions take place only within lower and upper critical conditioning factors. For instance, the germination of seeds, the activity of roots and rhizomes, the permeability of protoplasmic membranes, the rate of absorption and chemical action during growth in underground organs, must be greatly affected by the actual extreme temperatures encountered, as well as by the rapidity with which changes in temperature occur. The diurnal and seasonal temperature changes in the peat soil, and the differences in temperature between the aerial and underground portions of plants cannot fail to be of equally great importance in the physical and chemical processes, in the activity of the soil organisms on those biological changes which modify soil productiveness, and in the reciprocal physiological influences upon which absorption, transpiration, and transport of solutions from one part of the plant to another depend. The task of securing a coordination between these functions must be indeed a complicated one, varying greatly in different species according to their capacity of endurance. It is therefore clear that conditions as regards efficient temperature determine greatly the physiognomy of the individual plant and of the whole of the vegetation in habit of growth and distribution. But the rôle

which temperature plays quantitatively and qualitatively in the distribution of bog plant societies is in the main not known. So far as the writer is aware, no quantitative measurements between temperature as a probable causative or limiting factor and the resulting function and form in bog plants has been previously conducted, such as would afford any definite record of the actual physical conditions obtaining at different substratum levels in a bog vegetation. What has been said for temperature holds true also for evaporation. The influence of this and other factors is among the pressing problems of physiological ecology. From this point of view the data presented below have been collected in the field during the past three years.

The physical factors which modify and more or less control the community of plants on Cranberry Island have been formulated for the most part quantitatively. Yet it must be frankly admitted that, at the present time, interpretation of the data thus far gained is still only in part possible. Though the data have been gained laboriously through many months, and to the writer seem convincing, to attempt to correlate these accurately may be ill-advised. Only by the multiplication of such data will it be possible to express the results with quantitative exactness. The very necessity, however, of recording and accumulating an extended series of comparative observations is the justification of publishing now the data at hand. The conclusions here expressed, therefore, are still tentative, and true for the local investigation only.

Frequently the writer's students have assisted in this work, and acknowledgment is due to Messrs. L. W. Sherman, E. Wright, E. Linn, L. King, and M. G. Dickey for efficient aid. The warmest thanks of the writer are expressed here also to Professor J. R. Chamberlain, who surveyed the island, to Professors N. W. Lord, W. E. Henderson, and C. W. Foulk for cooperation in the chemical analyses, and to Miss F. Detmers for identification of plants and the care with which the floristic study has been generally furthered. The expense of the field work has been covered in large part by a special grant from the Emerson McMillin Research fund.

The habitat

The field work which forms the basis of the present paper was carried on at Buckeye Lake, Ohio. The geological record of the region is for interest second to few places in Ohio. The strata furnish an almost unbroken narrative from the Silurian up to the Tertiary. It is a rare thing to find peat bogs in Ohio south of latitude 40°, and this circumstance makes the locality as the southernmost limit of existing peat formations still more interesting.

Fig. 1.—Topographic map of Buckeye Lake and vicinity; U.S. Geological Survey, 1907; contour interval 20 feet (6 m.); scale, 1 inch = 1 mile (2.5 cm. = 1.6 km.).

ing. And to complete the panorama of the great past, the remains of the moundbuilders found near Newark, Jacksonville, and other places in the vicinity continue the record down to the historical period.

Buckeye Lake is situated in Licking, Fairfield, and Perry counties, about 26 miles (41 km.) east of Columbus, and is at an elevation of 150 feet (45 m.) above that of the University campus. The area and location are shown on the Thornville sheet of the U.S. Geological Survey (fig. 1). The lake, like many others, is one characteristic of the highlands of watersheds throughout Ohio and adjoining states. The heath bogs in Wyandot County, the extensive bogs in Huron County, possibly among the largest

peat deposits in the United States, the Pymatuning tamarack swamp in Ashtabula County are similar members of this interesting chain of water basins marking the less perfectly drained summit of divides. The depressions on such summits receive water which creates no surplus and hence has almost no eroding powers. Buckeye Lake is now an extensive body of water, about 10 miles (16 km.) long, and one mile (1.6 km.) wide, but was originally a pond in the glacial drift, containing approximately 595 acres (238 hectars). Its chief water supply today is the south branch of the Licking River.

The lake basin lies near the southeastern margin of the terminal moraine. The main western member of the morainic system is about 3–5 miles (5–8 km.) in width. It presents marked differences in topography, the closely aggregated knolls and ridges rendering the belt readily distinguishable from the bordering plain. The knolls are generally conical in form with gentle slopes, ordinarily about 25–100 feet (7.5–30 m.) in height. These knolls were apparently formed at the time the gravel plain was being built up. They are thought to indicate that the head of the gravel plain was built up as a submarginal deposit to about its present height before the ice sheet had withdrawn from over it (**20**). The lake basin under discussion resulted from the comparatively slow retreat of glaciers and the consequent greater deposition of glacial material about the edge of a body of ice in an old glacial drainage channel. The "kettle" is characterized by comparatively steep slopes. Up to 1832 the lake was surrounded by about 3000 acres (1200 hectars) of swamp land covered with large trees (fig. 2). The report of Captain CHITTENDEN, as quoted by GRAY (**15**), gives the area of the lake at that time as 3300 acres (1320 hectars), which agrees very closely with its area as determined by later surveys. The present lake was formed in 1828 and completed in 1832, to serve as a reservoir for the Ohio and Erie Canal. The surface water was raised about 8 feet (2.4 m.) by forming a dike around the west end and a part of the north side of the swamp. It was hoped to supply the Ohio Canal with water from Newark to Little Walnut Creek, south of Lockville, a distance of 31 miles (5 km.), and the deficiency between Little

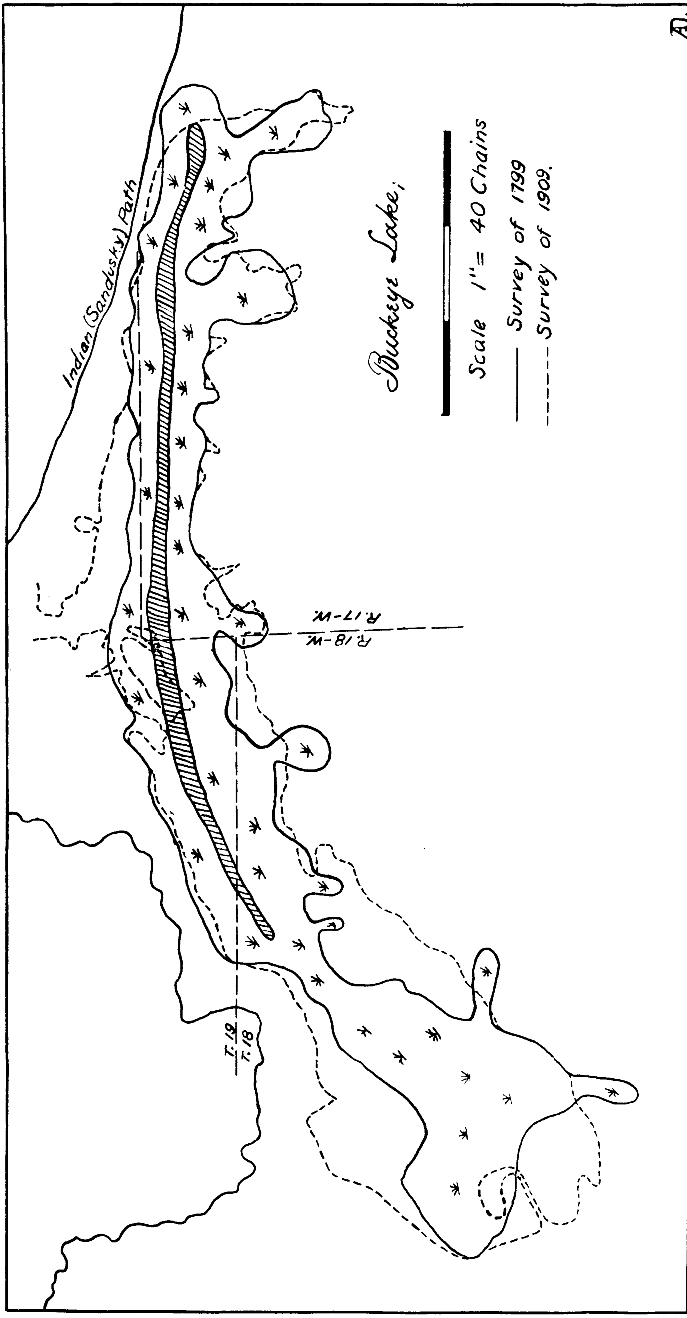

FIG. 2.—Buckeye Lake in 1799 and 1909; from tracings of the survey maps in the State Auditor's office at Columbus, Ohio.

Walnut Creek and Lockbourne. The reservoir soon proved inadequate for the canal, and in 1834 about 700 acres (280 hectars) were added, forming its present area. Its watershed embraces about 90 square miles (2331 hectars), which cannot be greatly enlarged. The lake then known as Licking Reservoir has, however, never stored a sufficient water supply and is not used for transportation purposes now. A large number of trees then standing soon died and fell into the water, where they remained beneath the surface. The majority of the trees were gradually cut away with

FIG. 3.—Cranberry Island; the view is from a hill northwest of the island near Buckeye Lake Station; to the left the woodlot; in the distance members of the terminal moraine; photographed August 1910.

their stumps exposed during low water. Only recently (the winter of 1908) the greater part of these stumps has been removed.

Near the northern bank of the lake, about one-half mile (0.16 km.) southeast of Buckeye Lake station, is the bog island, approximately one-tenth the dimensions of the lake (fig. 3). In position it is more or less sheltered by hills and a woodlot. The peat mass rises and falls with the changing water level of the lake, and supports a vigorous growth of trees, low bushes, sphagnum mosses, and cranberrries. Borings were made at various points on the island with a sampling tool devised by DAVIS (**2**), to determine the depth and the character of the peat. About 50 soundings were made, which indicate an average depth of peat of 30–35 feet (9–10 m.) along the southern shore of the bog island, and 11 feet

(3 m.) of peat along its northern shore. Borings made to the depth of 40 feet (12 m.) at the southernmost points of the island, and in the lake south of it, failed to reach bottom. The following table (I) gives some of the borings and related observations. The borings were made at a time when, for purpose of repair, the water surface of the lake was lowered 5 feet (1.5 m.) below the normal niveau.

TABLE I

ANALYSIS OF PEAT SPECIMENS FROM CRANBERRY ISLAND, BUCKEYE LAKE, OHIO

Analysis nos.	Station	Depth ft.	Depth meters	Description of peat samples
5.....	Central zone; sphagnum-cranberry	5	1.5	Brown, fibrous peat; mostly cranberry, sphagnum, and sedges.
7.....		14	4.2	Brown, non-fibrous, plastic peat with diatoms and shell marl.
8.....		25	7.5	Dark brown, well decayed, finely granular peat; algae (?) and filling from marginal borders.
9.....		40	12.0	Nearly black, non-fibrous, clayey peat.
11.....	Maple-alder zone	6	1.8	Dark brown, slightly fibered peat, coarser fibered below.
12.....		10	3.0	Brown and fibrous peat.
14.....		18	5.4	Dark brown, well decayed, finely granular peat with shell marl.
21.....		31	9.3	Fine sand with clay underneath.
22.....	Northeast station	5	1.5	Brown, fibrous peat; mostly cranberry, sphagnum, and sedges.
26.....		18	5.4	Granular peat; very sandy above, marly beneath.
27.....		28	8.4	Sandy marl; blue clay beneath.
28.....	Southeast station	5	1.5	Brown, coarse fibrous peat.
29.....		10	3.0	Dark brown, slightly fibrous; a lighter colored coarse fibrous peat underneath.
30.....		20	6.0	Brown, fibrous peat containing roots and rhizome fragments.
31.....		40	12.0	Black, plastic, non-fibrous peat; bottom not reached.
32.....	Southwest station	5	1.5	Light brown, coarse fibrous peat.
36.....		20	6.0	Plastic, fine fibered, dark brown peat containing shell marl.
38.....		40	12.0	Black, plastic, non-fibrous peat; bottom not reached.
40.....	Northwest station	5	1.5	Light brown, fibrous peat, composed of sphagnum and other bog plants.
42.....		20	6.0	Fine fibered, dark brown peat.
45.....		28	8.4	Sandy gravel underlain by blue clay.
48.....	Lake station	6	1.8	Dark brown, slightly fibrous peat.
49.....		40	12.0	Black, plastic, non-fibrous peat; bottom not reached.

It will be seen that the accumulation of vegetable matter has been sufficient to cause the lake basin to be filled with a layer of peat of considerable depth. The deeper strata have been reduced by humification, largely to the form of a black humus, a semi-liquid muck. The fineness of grain and the peculiarly soft consistency of it suggest that it is in part made up of the remains of algae, and in part a filling from the border of the lake, spread over the bottom. The upper strata are lighter in color, and very fibrous, loosely felted in structure, and have a matted appearance. As the island is sounded through from top to bottom, the samples brought up show a progressive change in color from light to darker shades, and in texture from coarse and loose to fine and more compact peat always saturated with water. In some places this sequence is repeated, that is, below the peat muck occurs a second fibrous brown layer followed by muck or clay. The escape of gases is very noticeable during the test borings, and also the staining of the brass peat sampler to a bluish-purple bronze, indicating the presence of a gas like hydrogen bisulphide. Only a small deposit of shell marl has thus far been found underlying the peat substratum in places. The Characeae and Cyanophyceae concerned with this process (**10**) are not abundant enough to be considered as agents in the aggradation of the basin. The lake bottom is of clay and in places somewhat sandy. The thickness of the deposit of peat in this morainal depression indicates, therefore, that the vegetation must have obtained an early foothold.

The chemical analysis of the substratum

The drainage of the bog island is merely that due to seepage through the porous peat. Ordinarily very little water passes either into or out of the bog island, except at such times when the water level of the lake fluctuates with extremes in precipitation or from interference in drainage. Even then the seepage is not rapid. The amount of salts dissolved in the lake water which is retained by absorption in the humus soils along the margin of the bog island is relatively small. The analyses show a total mineral content of 4 and 9 parts per hundred for the central and marginal zones respectively. Average samples of the air-dried peat taken

at a depth of one foot (30 cm.) from the surface layer give the following chemical composition (table II). For purposes of comparison analyses have been added of peat soils from a tamarack bog near Edgerton, Ohio (station VII), from a bog near Orrville, Ohio, now under cultivation in celery, onions, etc. (station VIII), and from a peat bog under cultivation, the soil of which is reported as unproductive (station IX).

TABLE II

CHEMICAL ANALYSES OF PEAT SAMPLES

Constituents	Sphagnum-cranberry zone	Maple-alder zone	Tamarack zone	Cultivated peat	Diseased peat
Volatile matter	60.90	68.91	60.50	52.47	52.56
Fixed carbon	22.19	19.60	26.84	23.98	19.35
Ash	7.68	3.56	3.30	14.70	19.42
Sulphur	0.12	0.00	0.20	0.39	2.21
Nitrogen (equivalent to ammonia)	0.80	2.55	1.51	2.58	2.38
Potash (K_2O)	0.12	0.12	0.15	0.31	0.64
Phosphoric acid (P_2O_5)	0.03	0.03	0.29	0.34	0.37
Insoluble	0.00	0.00	0.15	0.07	0.15
Available	0.03	0.03	0.14	0.27	0.22

It appears, therefore, that where peat varies from a highly fibrous condition, light brown in color, as in the sphagnum-cranberry zone, to a structureless condition, i.e., well decomposed, only slightly fibrous, and dark brown in color, as in the maple-alder zone, not only the physical constitution but also the chemical composition is highly variable. The determinations, which were made in the same way as fertilizer analyses, show conclusively that from the standpoint of available plant food constituents, the peat of the maple-alder zone is superior to that of the central sphagnum-cranberry zone. The analyses of peat ashes indicate only a small fraction of a per cent of potash and of phosphoric acid, but a fairly large amount of the valuable nitrogen ingredient. Preliminary work indicates also that the relative availability of the peat nitrogen seems at the most 8 to 12 per cent; but that this relative availability of peat nitrogen is considerably increased when the peat is composted with the bacterial life from stable manure, the peat from the central sphagnum-cranberry zone dis-

integrating, however, less readily than that from the maple-alder zone.

The reducing action of peat soil

It is a well known fact that fresh samples of bog soil upon exposure to the air extract oxygen from the air with great rapidity. Soil-sampling tests show that this power is strong in the cranberry-sphagnum peat, reaches a maximum in areas where the peat substratum is compact and less coarsely fibrous, and decreases as the border zone along the margin of the lake is reached. Judged by the quickness with which the soil becomes colored, and the intensity of the color, reducing processes increase on Cranberry Island from any marginal point to the central zone, and decrease as the opposite shore is approached. Reduction action becomes greater with the depth of the deposit.

The reducing power of the soils is shown clearly by the addition of a starch iodide solution. The observable action is variable, as already mentioned; the blue color disappears rapidly in soils from the cranberry-sphagnum area; the solution is greatly lightened with soils nearer the margin of the lake; no action is detected with soils along the margin. Various dyes such as lacmus and methylene blue and other coal tar colors decolorize similarly. Possibly the absence of sulphur in the analysis of maple-alder peat (table II) is due to the complete conversion of sulphur to hydrogen sulphide. This gas is the product of a reduction and has been detected by means of lead acetate paper.

Whether the reduction power in peat soils is produced by microorganisms, is due to enzymes, or caused by external chemical or bacterial metabolic products, these tests fail to show. Nothing absolutely certain is known regarding the composition and the nature of reducing substances. They have not at present been very fully studied by ecological workers. Apart from their destruction by aeration, tillage, and heat, and their adsorption by insoluble substances such as quartz, kaolin, carborundum, lamp black, and others, uncertainty exists as to whether the reducing bodies in bogs are unsaturated compounds comparable in properties to unsaturated fatty acids, to substances which possess the characteristics of certain organic reducing ferments, or to

residual by-products of an incomplete disintegration of peat. They unquestionably reduce oxygen-containing compounds in contact with them; their action is most marked where micro-organisms play a part in decomposing organic matter; the amount reaches, it seems, a maximum in early autumn. It should be stated further that toxicity and the reducing action of peat soil and that of the decomposing organic matter which retards oxidation in the soil are not necessarily the same phenomena. An increase in the amount of oxygen does not always decrease toxicity or the reducing power of the soil, and hence the amount of oxygen absorbed cannot be taken as the measure of the total action of these conditions.

Reduction processes are predominant in the early stages of peat formation, but are less manifest as the concomitant plant societies are succeeded by others, and especially when deciduous forests prevail. The same factors which decrease the toxicity of the habitat and the accompanying reducing processes favor an increase in the rate of oxidation and influence thus the character and nature of the succession. The greater oxidation, therefore, in the known productive peat soils would seem to be due to the activity of a different set of microorganisms, which by enzymotic action or otherwise hasten the formation of compounds of an assimilable nature. The excessive oxygen avidity of peat soils in the early formation stages must undoubtedly be injurious to plants, unless the plants, indigenous or invaders, are likewise able to exhibit oxidizing or reducing powers. The reducing processes in a soil very likely activate oxidative powers in plants. The various reactions of fungi, micorhiza, alder tubercules, bacteria, and the roots of higher plants growing in peat and humus soils should on that account be made the subject of considerably greater and more detailed study. The consideration of the relation between plant societies, relative physiological aridity, and micro-organisms, with their reductive and oxidation processes in soil has scarcely passed beyond the theoretic field of speculation. And yet it is this relation which makes soil problems especially interesting and in need of experimental work of considerable scope (**28**).

The bog water is relatively clear, the suspended particles imparting to it a slight tinge of olive green to brown. The analysis of samples of bog water and lake water give the following results (table III).

TABLE III

CHEMICAL ANALYSIS OF BOG WATER AND LAKE WATER FROM CRANBERRY ISLAND

Constituents in parts per million (May 30, 1910)	Bog water, central zone (cranberry-sphagnum)	Lake water
Nitrogen as albuminoid ammonia	10.34	4.50
Nitrogen as free ammonia	5.19	2.95
Nitrogen as nitrites	0.0005	0.0000
Nitrogen as nitrates	0.20	0.10
Chlorine	0.30	1.00
Required oxygen	71.80	3.70
Alkalinity (as $CaCO_3$)	30.00	75.00
Incrustants (as $CaCO_3$)	74.00	76.00
Total solids	140.00	200.00
Loss on ignition	100.00	4.00

Examining these results, shown in table III, we find that the lake water contains organic matter in a state of advanced decomposition. This is indicated by the relatively high free ammonia, and the small amount of oxygen consumed. The reverse holds true for bog water from the sphagnum-cranberry zone. In other points lake water agrees well with bog water. The osmotic pressure and the acidity have been found to be the same for both stations. As compared with the freezing point of pure distilled water, the average lowering in the various determinations is 0°007 and 0°009 for the central station and the maple-alder and lake station respectively. Acidity varies from less than 0.00075 to 0.0038 normal acid when titrated with a $n/0.05$ NaOH solution. The soil is alkaline at depths near the marly subsoil. The stress laid by various authors upon the relation of these two factors to plant societies in bogs, in so far at least as this region is concerned, will not hold. They are not factors in the selection or distribution of species for bog habitats.

Physiological properties of bog water

The physical and chemical sides are found unsatisfactory to explain the functional variations and the pathological changes

in structure which agricultural plants undergo when growing in peat and bog water. Elsewhere it was shown by means of transpiration data of cultivated plants, and with a biometric study on the annual wood-increment in the red maple found on the island and in woodlots near the shore, that (1) a difference exists between different species in their power of resistance to the toxic action of the substratum; (2) the contrasts in the relative growth of plants vary with the substrata of the several bog plant formations; (3) the toxic principles whether enzymes or other bodies are not found in bog water when attempts are made to extract them with insoluble adsorbing bodies; they do not pass readily through filters and only slightly through filter paper; (4) different physiological phases result from the progressive addition of an adsorbing substance; (5) agricultural soils used as filters decrease considerably the normal physiological activity of plants growing in them; (6) the reduced absorptive capacity of the plants is not a consequence of the absence of root hairs, or of a smaller absorbing surface.

The bacterial flora of the peat substratum

Present writers seem to hold the view that among the simplest of fungi, the Schizomycetes, few are present in peat bogs, and that only a small number of species, included in perhaps only one family, are at all injurious to higher plants. Examination has shown that peat soils contain unsuspected groups of bacteria, which in number and efficiency vary during the seasons and with the several plant zones on the island. As a means of differentiation between the bacterial flora of the plant formations, studies were made on the action of the bacteria in 0.5 cc. bog water upon various culture media in fermentation tubes. Soil water solutions were collected in sterilized glass-stoppered bottles from each of the following stations: station I, lake water; station II, marginal zone (*Decodon-Typha-Hibiscus*); station III, cranberry-sphagnum zone, 1–3 feet; station IV, same, 3–5 feet below surface vegetation; station V, maple-alder zone, 1–3 feet; station VI, same, 3–5 feet below surface vegetation; station VII, tamarack soil from Edgerton, Ohio; station VIII, peat soil under cultiva-

tion from Orrville, Ohio; station IX, peat soil under cultivation, reported as unproductive and "sterile," from Lodi, Ohio; station X, humus soil from the university woodlot (beech-oak-maple-elm). The culture media employed for this work were a 1 per cent starch peptone water solution; 1 per cent solutions of cane sugar, dextrose, and lactose in beef broth; plain bouillon; plain and litmus milk; 0.2 per cent nitrate peptone water; Dunham's peptone solution for the indol test; nutrient gelatin and agar. Only the generally well known determinations, as of the breaking up of carbon and nitrogen compounds and the proportion of the various gases evolved, have been made. The chemical analysis of the soil samples of stations I to IX is given in tables II and III.

The culture studies gave the following characteristic results after an incubation period of 5 days at 38° C. The action of the bacteria on starch shows in several stations the production of an inverting ferment by the cultures. The starch is changed into a sugar which reacts with the Fehling's test. In stations III and IX there is no action; in stations II and X the conversion is carried on a little way and then stops, there being always a red or purple reaction with iodine; in station I the starch conversion is almost complete; while in stations IV, V, VI, and VII certain putrid by-products inhibit in various degrees further conversion. Upon the addition of a few drops of potassium iodide, the blue color disappears rapidly in stations III, IV, and VI; the hydrated iodine is deposited as metallic iodine upon the walls of the test tube above the solution. Reduction action is less active in stations V, VII, and IX. No decolorization occurs in stations I, II, and X. The accumulation of iodine is very strong in the test tube of station X and is very likely an indication of the presence of oxidizing ferments. With methylene blue the reduction action is the same in degree, respectively, in all cases running parallel with the iodine action.

In all stations, with the exception of station I, the action of the bacteria on saccharose shows both the conversion of the carbohydrate into glucose by the inverting ferment, and the production of gas and acid. The reaction is strongest in stations VIII and X; relatively small in stations V and IX; very little gas is evolved

in station II. The gas is largely hydrogen gas and CO_2; the latter, with the exception of stations V and VIII, is present usually in small quantities and was distinguished from other gases by its absorption in sodium hydroxide. Fermentation action is shown better on dextrose and lactose. There is little growth and gas formation in station I; no acid is produced in stations VII and IX; and very little hydrogen gas is formed in station VIII. In all cases the growth of the organisms produces a marked and varied pigmentation in the solutions.

In plain milk, rapid coagulation precedes further bacterial action in all cases except station IX, in which coagulation occurs very slowly. Milk is slowly peptonized anaerobically in stations IV, V, and VI; surface digestion takes place in stations III, VIII, IX, and X; it is rapid in stations I, III, and VI; and gas is produced in moderate quantities in all stations except station VIII. Litmus milk is coagulated in all stations; the medium gradually decolorizes and the cultures become acid in various degrees; the color does not return upon steaming the test tubes. With a majority, gas is produced in various amounts during digestion, except in station IX, in which the bacterial reaction is faint though strongly odorous.

On bouillon bacterial growth is slow; it is never very turbid or heavily clouded, and only in one case, station IX, gives a whitish precipitate.

The power of indol production is greatest with the organisms in stations III, V, and IX; the action is relatively small in stations II, IV, VI, and VII; and present to a feeble extent only in stations I, VIII, and X when tested with 0.02 per cent solution of potassium nitrite and sulphuric acid.

The ability to form nitrites from nitrates in nitrate broth is common to the organisms in all stations. The amount of nitrites formed is high in stations IV, VI, IX, and X, and very small in stations I, II, VII, and VIII. The power to reduce nitrates to nitrites is not present in the same degree as noted above for the reduction action in starch media. It is certain that the microorganisms are capable of reducing nitrates, but to some extent metabolic products, apparently, modify the action. The test

was made with equal parts of sulphanilic acid and napthylamine solution.

The presence of ammonia was tested with Nessler's reagent. The reaction is stronger in stations VII and X than in any other station. A faint test is obtained in station IX. Nitrogen gas is produced from nitrates in stations VII and VIII.[2]

Before summarizing the facts brought out in the culture studies, there is need of mentioning another matter. A knowledge of the morphology of the simple form of organisms does not suffice to differentiate the numberless more or less similar species. It is difficult and almost impossible to identify a distinct and constant type for each species, or recognize form-differences suitable for classification. Nor does it seem that culture methods have made possible systematic grouping, or the variety of tests needed for accurate and trustworthy comparisons. No necessity exists for doubting the value of cultural characters; it is merely maintained here that additional and new methods must be tried, and tests should be scrutinized from every standpoint. Though widely different in their behavior in culture media and in their relation to air, yet the pathogenic properties of the bacterial flora from the different plant formations and societies should be ascertained within the limits of their natural habitat, and should be determined also with reference especially to the degree of functional inhibition on higher plants. It is not until a study is made of the special reaction of bacterial transformation products in sterilized bog water upon the growth of agricultural plants that the lack of salient features between habitat relations and physico-chemical reactions in artificial media becomes noticeable. Considerable difficulty was experienced in the isolation of organisms with the conventional media. In the majority of cases very little growth was obtained on beef broth gelatin or agar. Gelatin and agar media made with peat and bog plant juices proved more satisfactory for isolation purposes. Moreover, bacteria of rapid growth and early appearance of colonies on the artificial media

[2] Since the observations herein recorded, the writer received through the courtesy of Professor HARSHBERGER a paper published by Dr. D. RIVAS on "Bacteria and other fungi in relation to the soil" (Univ. Penn. Publ. **3**:243–274. 1910). It is cited here as bearing directly on the problem in hand.

caused less retardation on the growth and transpiration of wheat plants when inoculated into sterilized bog water than bacteria of slow growth. In some cases the isolated pure cultures made little headway on beef broth or peat agar media after a period of 3–5 months, but gave strong inhibition in the growth of wheat plants within 3 weeks after inoculation into sterilized bog water from their respective plant zones. It is reasonable to assume, therefore, that the lack of uniformity in results implies both obligative symbiosis and the need of a physiologically balanced culture medium. The fact that the organisms are obligate saprophytes, capable of growing only on substrata similar in composition to the character of the surface vegetation, is indicative of a close interdependence; their rapid growth in a medium in which cellulose and lignin compounds predominate suggests a specific cytohydrolytic action. Certain microorganisms in station III have been found to possess the ability to dissolve filter paper, but their isolation has not been successful.

It is needless here to repeat the physiological tests which were made with a number of isolated pure cultures inoculated in sterilized bog water. Transpiration figures of wheat plants growing in these solutions and various other data have been published in an earlier paper (*l.c.* 9) to show the active participation of the organisms in the formation of bog toxins, and their ability to inhibit during the processes of denitrification and dehydration the growth of plants alien to the habitat. With these suggestions in mind, the results on the bacterial reactions in culture media submitted above may now be summarized as follows:

Peat soils are very rich in bacteria inducing diastatic, inverting, proteolytic, cytohydrolytic, and reducing action.

The organisms vary in kind and number with the nature of the substratum.

The majority of the forms are found to thrive as saprophytes, digesting the débris in the upper layer of the peat substratum and aiding in a partial disintegration of the accumulating deposit. Many forms thriving as saprophytes among the indigenous flora give little aid in the elaboration of food materials to invading or introduced plants.

The organisms show a marked interdependence between themselves; one set of bacteria prepares a medium for another out of an unfavorable substratum, and this paves the way for others to continue the destruction. Signs are not lacking, however, of relative indifference and even antagonism among the organisms, resulting in products which retard and inhibit further bacterial growth and disintegration processes.

A certain proportion of bacteria in these soils has the special ability to produce substances, perhaps unassimilable, certainly injurious to all but indigenous plants. In a peat substratum the percentage of bacteria aiding in the production of deleterious substances such as reducing bodies, gases, indol, and other fermentation products varies with the season of the year, but especially with the advance of the vegetation toward the closed deciduous forest formation. These bodies constitute the unsanitary conditions in soils, the negative factor which limits the rate at which the splitting up of organic compounds into ammonia and other assimilable substances proceeds. They are the characteristic symptoms of a diseased, sterile soil. The greater oxidation in the productive peat soil is due to the activity of a different set of bacterial organisms. The rôle which microorganisms play in the soil points, therefore, to the fact that among other things a considerable relation exists between the processes of disintegration of organic material and the succession of plant formations in bogs and marshes, and in peat soil under cultivation.

Each plant formation has its own bacterial flora maintaining a physiologically balanced condition in the soil. The substratum of each plant formation is an ever varying medium, the seat of physical, chemical, and vital activities which directly and indirectly influence its relative fertility and the character of the surface flora. Varying with the power of multiplication and metabolic activity is the quantity of the products of decomposition constituting a toxic, physiologically arid habitat at one phase, and an available supply of nutrients to plants at another stage of the process. Acidity, toxicity, and reduction action represent merely a stage in the decomposition of organic matter. In the natural successions which ensue, each plant association augments the

efficiency of the soil as a habitat. The soil processes involved are an efficient natural process for the maintenance of relative productivity. Differences in the mineral components are trifling compared with the biological processes.

The sum total of the reactions in any stage of the process exercises a physiologically selective function upon invading plants, furthering the growth of such plants whose roots are not merely absorbing organs, and excluding and eliminating all others in which the power to make extracellular changes in the soil is inefficient.

The significance of the data calls, however, for still further experimentation to be of sufficient evidence to assume a specific metabolism in bog plants, or to disclose the chemical nature of bog toxins.

Origin of the habitat

Initially the bog island was formed as are all bogs occurring in glacial moraines, or in depressions which form frequently in the gravel plains along the lines of drainage from the front of the glacial ice. Extensive acquaintance with peat bogs or a comparative study of the lists of plants from different regions will convince any careful observer that bogs are very different in character, and that not all of them have been formed in the same way. There may be a number of possible ways by which such accumulations of vegetable matter came about. Various such points of view and methods of classification have been suggested in a comprehensive study by DAVIS (**11**). As the process of bog development here seems similar to that of the peat deposits which the writer has observed at Michigan, the following brief account is given.

During the glacial period, most species common to bogs skirted the border of the ice sheet. Whatever plant or animal life existed was confined to the highlands east of the Scioto Valley, south of the Ohio River, and in the southern portion of this continent. At the margin of the ice sheet the conditions must have been quite circumpolar in character, similar to those of the barren grounds of the far north, that is, there prevailed short summers and long winters with frequent winds and storms. Whatever the causes

that resulted in such climatic conditions (4) with their change and with the progressive northeastward movement of the ice, an increasing land area became exposed, the topography of which is even now largely the inheritance of that time. While yet the entire surface of northern Ohio and the land north of it was buried under the ice sheet, the region about Columbus and Buckeye Lake was among the first to be laid bare by the retreating ice and water. The receding of the ice sheet was paralleled by the northeastward movement of more favorable weather conditions which initiated a migration northward of plants and animals along the glacial drainage channels, the earliest highways for the dispersal of many forms of life (1). As the ice and water continued to recede and the processes of erosion brought about better drainage and lower water levels, the flora and fauna followed down the slopes and began to encroach upon the ponds and lakes. The bog plants and their associates slowly had passed northward close to the base of the retreating ice, and hence were among the first to take possession of the new territory.

As has been stated, the test borings make it evident that the bog vegetation grew out from the shores, forming a floating mat; that sphagnum and cranberry appeared after the sedges and rushes had built up the surface mat; that filling in of débris from the sides continued slowly until the water had become shallow enough in places to enable shrubs and trees to occupy the area. The later phases of mature bog forests the writer has met very frequently in Ohio, and several interesting localities have been studied in connection with an inquiry on the peat deposits made for the Ohio Geological Survey.

While it is not clear how the preservation of the local bog island has come about, the present investigation has led to the conclusion that a well marked relationship existed between the type of peat soil considered with regard to its degree of disintegration, and the succession of plant associations covering it. As elsewhere in Ohio today, the firmer and well decomposed peat strata were covered sooner with forests, and were built up rapidly by an attendant sinking and shrinkage of the mat under the added weight of the growth and fall of trees and the vegetation of suc-

cessive seasons. On the other hand, the absence of logs and fallen timber in the peat of the sphagnum-cranberry zone points clearly to a relatively slow encroachment upon the open water by the plants. When inundation took place, only the coarsely fibrous and incoherent cranberry-sphagnum mat rose with the water level, and its vegetation survived.

As late as 1830 the bog was an extension from the mainland. After the formation of the dike, and the consequent rise of the water level, most of the mainland became inundated, leaving the bog completely an island. With its surface vegetation of mostly northern forms, the island is virtually a water culture on a large scale. None of the plants are dependent for any important part of their food on the mineral soil below the peat. Cranberry Island is, therefore, not to be considered merely as a case of the conversion of a forest into a marsh under the influence of an increased water content in the soil. The analysis of peat samples shows that the vegetation now growing upon the peat substratum represents quite fully a continuation of the former boreal flora. It presents today a somewhat disjointed distribution, but this has come about chiefly through recent repeated disturbances in the water level of the lake, through a settling and shrinkage of the peat soil, through the slow encroachment of the invading southern vegetation, and through the formation in places of a better and firmer soil.

The flora

For convenience three well marked plant zones may be pointed out, each of which is characterized by communities and groups of plants easily differentiated from the others. No attempt has been made to give full lists of plants, or to correlate the associations and successions mentioned with similar conditions elsewhere. Essentially the same order of succession and of arrangement of plants as has been described for northern bogs is not, of course, to be expected. The species are not always the same in the corresponding formations, but they are systematically related and closely similar in ecological structure.

A fuller floristic treatment is now in preparation, in which many of the features are described in detail.

THE BORDER ZONE

The outermost growth which immediately borders the open water and forms a more or less broken fringe around the island is for the most part hydrophytic. Along the southern shore it is dominated by the swamp loosestrife (*Decodon verticillatus*) and in places by cat-tails (*Typha latifolia* and *T. angustifolia*). This facies has for its principal and secondary species *Hibiscus Moscheutos*, *Sagittaria latifolia*, *Polygonum hydropiperoides*, *Ranunculus pennsylvanicus*, *Scutellaria galericulata*, *Lathyrus myrtifolius*, *Bidens cernua*, *Potentilla palustris*, *Campanula aparinoides*, *Galium triflorum*, *Cicuta bulbifera*, *Peltandra virginica*, and others. They are generally abundant, with *Decodon* and *Typha* forming a dense growth, which attains a height of 2–6 feet (0.6 to 1.8 m.) above the substratum. The vertical zonation is that of the differences in habit of growth of the individual species. The members differ widely from one another both in external features and in their demands upon the environment. In these regards the vegetative shoots adapt themselves little to the prevailing exposed conditions. Growing upon a peat substratum whose depth and physical characteristics are in every way like that of the other plant zones to be described below, the xerophytic type and quality are least marked in this vegetation. The well decomposed peat soil of the border zone permits here a luxuriant growth. The plants are able to secure all of their raw food materials from the water and air, and build their own substratum. The high water capacity of peat, the absence of a mineral soil, the smaller percentage of oxygen in the water, and the incoherency of the substratum afford no precarious conditions for growth. Here the toxicity of the substratum and the consequent physiological aridity are least marked. It is evident that dilution and the capacity of absorption of soluble salts by the humus soil along the margin (**8**, p. 403; **9**) corrects any harmful effect.

The *Decodon-Typha* association has a transition appearance, for a considerable admixture of plants such as *Rosa carolina*, *Cephalanthus occidentalis*, *Cornus canadensis*, *C. paniculata*, *C. stolonifera*, *Salix discolor*, *S. nigra*, *S. pedicellaris*, *Alnus incana* (?), *A. rugosa*, *Ilex verticillata*, *Prunus melanocarpa*, *Rhus Vernix*,

and various secondary dependent associates, occupy the firmer parts of the marginal zone and form an almost continuous fringe, the *Alnus-Rhus* association. In places it extends diagonally across the bog island as scattered dense thickets (fig. 4). This community of plants presents on the whole very little zonation within itself. It constitutes a zone of varying width, 5–30 feet (1.5–9 m.) and more, and attains a height of 8–12 feet (2.5–3.5 m.). Only in a few places along the southern shore this type of bog shrub formation is absent altogether and is replaced, as has been

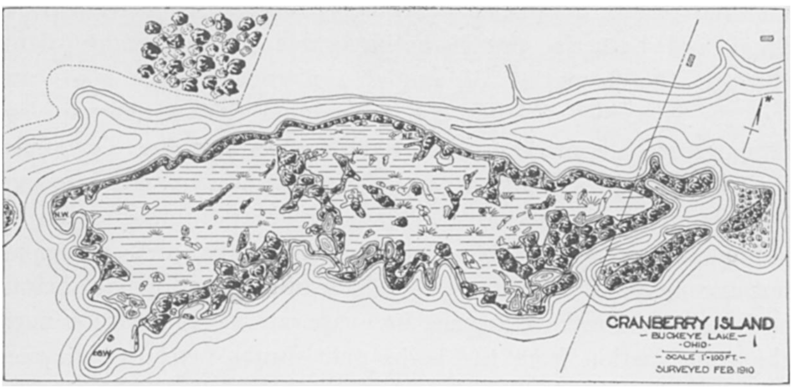

FIG. 4.—Map of Cranberry Island; surveyed February 1910; the divisions into plant societies as indicated by the map and the text are based on general characters of the vegetation; Δ, *Decodon; T*, *Typha;* the ponds on the island are shaded.

stated, by *Decodon* and *Typha*. The edaphic conditions of this part of the habitat seem to approximate those of the undrained swamps as described by COWLES (**6**). Nearer the lake there is a tendency toward the segregation of *Decodon verticillatus* and *Hibiscus Moscheutos*. Of the two, the former is more vigorous and occupies the deeper water. *Rosa carolina* prefers the outer border also, but clings quite closely to *Alnus incana* and *Cornus stolonifera*. Contemporaneous with the thicket-formers, various species of lianas invade the association. The mature thickets are often covered with an impenetrable growth of tangled vines of *Apios tuberosa*, *Solanum Dulcamara*, *Convolvulus Sepium*, *Ipomoea* sp., and *Cuscuta Gronovii*. *Cephalanthus occidentalis* does not

constitute a large part of the shrub formation. Together with *Decodon*, it is found frequently indiscriminately mixed with facies in the central zone. In fact, the differences in the formation are to be seen largely in the ratios between the numbers of individuals present, and not in their entire absence from either.

THE MAPLE-ALDER ZONE

With the maturity of the facies, a gradual change in the environmental conditions for the plants takes place. The annual leaf-fall covers the substratum with a visibly thicker layer of vegetable material rich in organic matter, and is followed by the growth of fungi and bacterial organisms favorable to succeeding plants through the formation of available nitrogen. Like snow and ice, the covering of fallen foliage reduces the extremes of soil temperature, suppresses the growth of *Sphagnum*, *Oxycoccus*, and similar plants from the adjoining central zone, and improves the production of a kind of humus of great significance to the animal life as well. Moles, earthworms, snails, and insects are not uncommon in this zone. The shade of the trees during summer and autumn checks extremes in evaporation, and thus reduces the transpiration from the herbs and shrubs beneath the trees. Through the combined action of these and various other agents, there is a corresponding rearrangement of some species and the disappearance of others. In places along the margin, the peat substratum is firmer, fairly well above the level of the lake, and comparatively better drained. These conditions are sufficiently established at the southeast side of the island to be characterized as the maple-alder zone. The bog tree formation is quite prominent, and though not extensive, it is still a strongly marked zone. The most conspicuous plants are large-sized maples (*Acer rubrum*), alders (*Alnus incana*, *A. rugosa*, *Ilex verticillata*), the chokeberry (*Prunus melanocarpa*), black cherry (*Prunus serotina*), and poison sumach (*Rhus Vernix*). Oaks (*Quercus palustris*, *Q. imbricaria*), ashes (*Fraxinus nigra*), and the silver maple (*Acer saccharinum*) are still relatively rare. The trees are surface-rooted. The roots do not penetrate to a depth of more than one foot (30 cm.). They spread out in all directions from the trunk, and are of sufficient

size and length to withstand the mechanical strains due to the action of air currents. The association is still an open community of plants and has four distinct vertical layers. The trees cast a relatively dense shade, in which grow seedlings and young trees of oak and maple, and a variety of shrubs and herbs. Most abundant are *Sambucus canadensis*, *Impatiens biflora*, *I. pallida*, *Rubus* sp., *Dianthera ovata*, *Viola blanda*, *Aspidium spinulosum*, *Osmunda regalis*, *Carex scirpoides*, *Aspidium cristatum*, *Habenaria clavellata*.

There is protection from strong air currents, and in the changed light, heat, and moisture conditions the plants offer a striking contrast to the vegetation next to be described. Many of the herbaceous and shrubby species occur only sparingly, and are really constitutents of the other societies of the border zone. In the numerous maple and oak seedlings the evidences are seen that the *Rhus*-alder consocies will not continue to occupy the habitat. The lowering of the water table due to the continued addition of débris and leaf-humus will hasten the advent of better soil, drainage, and shade conditions. *Alnus* and *Rhus* and their associates will find the new conditions unsuitable; they will disappear, leaving the zone more typically an oak-maple-ash formation. It is not probable that this coming society represents a climax forest for filled lake basins in this locality. There are limited portions on Cranberry Island which in the course of years are bound to revert to the central zone bog type, and that perhaps intermittently, for a settling and shrinkage of the numerous water pockets in the peat substratum will continue until all of the lower strata have become firm and compact. With continued accumulation of forest litter, the soil conditions will finally become drained and more xerophytic, to an extent that will constitute an ecological habitat considerably different from that existing in the neighborhood. Should the water level remain constant, the amount of upbuilding will be limited to the distance to which the water will rise through the accumulation of peat, and supply the growing plants at the surface with the necessary physiological water. It must not be assumed, therefore, that the development of a mesophytic forest could continue in the same direction indefinitely.

It is the lack of moisture, and not low temperature that will arrest the growth and reproduction of the plants concerned, and the disintegrating action of fungi and bacteria. This factor in plant growth, not previously important to the plants of the sedge, shrub, and thicket growth, then becomes operative selectively, leading to the establishment of a xerophytic plant association. At present, however, there is little indication of the appearance of an association of that kind; the climatic trend favors broad-leaved forests, and the supposed physiographic characteristics leading to a xerophilous climax association assume nowhere on the island any considerable importance.

There are conditions, however, which would indicate a reversion to a hydrophytic association. Adjoining the maple-alder zone on the southeast side are several extensive areas which do not respond quickly to changes in the water level; fig. 7 illustrates a part of such an area. Through the accumulation of vegetable débris, the replacement of air and other gases held in the mat by water, but especially through the increased load upon the surface of the mat after the heavier tree association became established, a settling and shrinkage of the peat occurred, which ultimately resulted in the sinking of the mat several feet below the water level. The cutting of the timber reestablished equilibrium and rejuvenation. The species now tenanting the mat indicate a tendency toward the development of a hydrophytic vegetation approaching the type of the border zone described. The marked difference between the vegetation of the central zone and the one establishing itself is worthy of special note. Except such portions of the fibrous mat as were long ago broken off from time to time by the action of wind and waves and drifted about as floating islands, the rejuvenated "sunken" mats, and such areas as annually rise in the early summer and disappear again beneath the water in late autumn concomitant with the "overturn" of the lake, show nowhere members of the cranberry-sphagnum zone. They illustrate most forcibly the fact that under these conditions a very different set of plants spring up and become dominant, although the true bog plants are near at hand.

THE CENTRAL ZONE

This zone is situated centrally on the island. It occupies the larger part of the area of the island, and in its floral structure is very distinct. The plants consist principally of *Vaccinium (Oxycoccus) macrocarpon* and several species of *Sphagnum*, with *Rhynchospora alba*, *Eleocharis obtusa*, *Aspidium Thelypteris*, *Dulichium arundinaceum*, *Carex comosa*, *Scheuchzeria palustris*, *Juncus canadensis*, *Eriophorum virginicum*, *Osmunda cinnamomea*, *Drosera rotundifolia*, *Menyanthes trifoliata*, several orchids, and other light-demanding forms variously grouped. The surface is characterized by hollows and elevations. The latter are due, in the opinion of the writer, to various causes; in part to the upward growth of sphagnum competing with cranberry, in other places because of a mutual protection which is afforded by the massing of forms of a similar height against excessive loss of water. In still other places, cranberry and sphagnum are growing beneath shade-producing forms, notably around ferns and invading maples and sumachs. Here they possess the ability to grow up in a manner giving rise to a thick soft mass, raised to a considerable height, more at the center than at the periphery. The maximum height to which cushions of sphagnum can grow is limited by the vertical saturation gradient of the water content in the air. The vertical level of this vegetation is otherwise fairly uniform, and varies only between 6 inches (15 cm.) and 1.5 feet (45 cm.) above the peat substratum, forming a low, dense, compact growth. The taller growth of grasses and sedges and the occasional bushes of *Gaylussacia baccata*, *Prunus melanocarpa*, and *P. arbutifolia* occur chiefly scattered and as open facies. They do not dominate the general vegetation enough to interfere with the transpiring organs of the plants at the lower level.

A more detailed study of the distribution of the species in the lower stratum shows habits of growth giving rise to vertical layers sufficiently defined to recognize vertical zonation; especially the differences of growth in height in the sphagnums, *Gaylussacia*, and *Vaccinium* in areas of varying physiological aridity show that the plants are adapted to a given average supply of water. But

in the zone under consideration, the differences in habit of form shade into each other, and in consequence are less distinct than those in the adjoining border zones. The prevailing grasslike growth-form, the general reduction in size of leaves assumed by the different species, is in harmony with the environment. It expresses itself not only in external features but also in the anatomical structure. As an ecological unit, the community of plants, identical in type, but different in floristic composition, exhibits well within itself the impress of its conditions of life.

FIG. 5.—A pond in the cranberry-sphagnum association; *Decodon* is the most important mat former making the advance upon the water.

Differences in aerial functions would be therefore largely species characteristics as well as environmental.

That the plants are adapted to a given average supply of available water, but with great specific differences among themselves, is further seen in the frail growth of *Cephalanthus* and *Decodon*, in the small trees of *Acer rubrum* and *Rhus Vernix*, and in the stunted forms of various other invaders from the neighboring plant societies which occur scattered throughout this zone. For the past few years thousands of maple, sumach, and alder seedlings have been observed to sprout, and yet failed to succeed beyond the first year's growth. Of those which succeeded, the stunted growth, the numerous dead branches, the ragged crown of foliage,

are a clear instance of the fact that the resistance offered by the invaders to the toxic conditions of this habitat is, indeed, but slightly effective.

There are several small ponds in the cranberry-sphagnum zone in which the dominance of *Decodon* and *Typha* as important members of the border vegetation is especially to be noted (fig. 5). *Decodon* is particularly well adapted in making an advance out-

FIG. 6.—The last stage of a larger water area, now occupied by the advancing cranberry-sphagnum association.

ward upon the water by the manner in which the slender mature stems, that bend toward the water, curve at the tips. From the submerged part roots arise in considerable numbers, buds form, and new plants develop. The young plants remain moored to the parent plant for a year or two. As soon as the stools are built, they become the habitat of a number of plants such as *Bidens cernua*, *Polygonum hydropiperoides*, *Cyperus strigosus*, *Impatiens biflora*, *Peltandra virginica*, and others. These with *Decodon* and *Typha* seem, however, unable to persist, for dead stems of *Typha* and remains of stools of *Decodon* may be seen in

the cranberry-sphagnum association immediately behind this border vegetation. The last stage of a former large water area now occupied by the advancing cranberry-sphagnum association is shown in fig. 6. Cranberry and sphagnum build a mat and tufts of great compactness and gradually overcome and eliminate the swamp loosestrife (*Decodon*), cat-tail (*Typha*), *Peltandra*, and others. The advance of the mat out over the surface, even of open water, can be demonstrated by a series of such stages and

FIG. 7.—A sunken mat in the process of rejuvenation; the increased load upon the surface of the mat, especially after the heavier tree association became established, caused the sinking of the mat; the cutting of the timber reestablished equilibrium.

"last vestiges" indicating the existence of concentric zones of *Decodon* and *Typha* in quaking mats where formerly water occupied the area (fig. 4). The mats are floating, for test borings through them end abruptly in water which is quite free from fibrous material. The space of open water between the upper mat and the rest of the deposit below has frequently a depth of 4–5 feet (1.2–1.5 m.). In several places the peat below such mats is fine grained and well decomposed, not at all of a character that would indicate a transition structure from the coarsely fibrous to the well disintegrated, slightly fibrous deposit resting on the coarser mat below.

The sphagnum-cranberry formation is not to be regarded as an intercalation (**18**). The organic matter deposited by past generations of plants shows that sphagnums, cranberry, and their associates occupied this surface long before the maple-alder zone was formed. It is therefore an earlier and normal stage of succession, under conditions of development and a combination of factors which favored persistence and succession in that direction, and which are not suitable even today for the ecesis of a shrub-formation or for germination and growth of the seeds blown over in great quantities from the woodlots and fields surrounding the lake.

The vegetation in the central zone agrees very largely with plant societies in bogs and swamps of more northern regions. Many other "boreal" plants which were no doubt concerned in the early developmental stages of the local bog are now extinct. This is especially true of the pitcher plant (*Sarracenia purpurea*), the creeping snowberry (*Chiogenes hispidula*), wild rosemary (*Andromeda polifolia*), leather leaf (*Chamaedaphne calyculata*), labrador tea (*Ledum groenlandicum*), pale laurel (*Kalmia polifolia*), and larix (*Larix laricina*). The plants are still found in Ohio bogs north of here. A number of them have been recently transplanted and are now on the island in good condition.

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